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PREDATOR-PREY BIOMASS FLUCTUATIONS IN THE PLIO-PLEISTOCENE

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ABSTRACT

The application of principles derived from recent ecosystems to paleoecosystems is an important tool for testing the universality of these principles, as well as identifying deviations that require further investigation. Here, we estimate the predator and prey biomass in nine Italian Plio-Pleistocene mammalian paleocommunities and compare their relationships with recent ecosystems. The predator-prey biomass relationship is shown to be identical in extant and fossil communities for prey species less than 450 kg body mass (BM), thus indicating that biomass fluctuations from prey to predators were similar in Plio-Pleistocene and recent ecosystems for this BM range. However, if herbivores of 450 kg up to 1000 kg were also accepted as prey, the predator-prey biomass relationship differs significantly between Plio-Pleistocene paleoecosystems and recent ecosystems. Herbivores within this BM range occurred after the early Pleistocene, whereas both smaller (<450 kg) and larger (>1000 kg) herbivores were present in all ecosystems studied. The results of this study suggest that fossil herbivores of this particular BM range were ecologically different from similar-sized extant populations and did not constitute regular prey species for the predators present. Their emergence was not accompanied by a corresponding increase in biomass of predators. Thus, middle-Late Pleistocene ecosystems were potentially controlled from the bottom up rather than from the top down. The results reported herein show how successive estimates of body mass, density, and biomass can be used to reconstruct paleoecosystems.

INTRODUCTION

Exploring trophic interactions within animal communities is important for understanding how ecosystems function spatially and temporally. Relationships between predator and prey in terrestrial ecosystems have received considerable attention (East, 1984; Skogland, 1991; Sinclair et al., 2003). Early field studies on large mammalian predators have yielded important insights into interactions of large mammal communities (Schaller, 1972; Kruuk, 1972; Mech, 1981) suggesting an intricate mechanism of top-down control by predators on prey number and abundance. Nonetheless, herbivorous mammals not only play the role of prey in terrestrial ecosystems, but their feeding activity also modifies vegetation. Thus, populations of herbivores can also be resource controlled (Sinclair, 1977, 2003).

Presumably, this complex dynamic, observed in extant terrestrial ecosystems, should also apply to prehistoric ones. Diversity and abundance of extinct species can be assessed to understand how ancient ecosystems functioned. The study of predator-prey ratios has motivated investigation of this premise using faunal lists of fossil localities (Van Valkenburgh and Janis, 1993). However, this approach requires identifying predators and prey with a high degree of accuracy to allow direct comparison with data on extant ecosystems (Warren and Gaston, 1992). Raia et al. (2007) clarified this point after detecting a decrease in the predator-prey ratio during the Late Pleistocene of the Italian peninsula and attributing it to an increase in diversity of

megaherbivores (mammals >1000 kg). Megaherbivores escape predation control in extant ecosystems (Owen-Smith, 1988; Sinclair et al., 2003; Hummel and Clauss, 2008). This phenomenon is likely to be applicable to the Quaternary as well (Meloro et al., 2007).

On the other hand, multiple lines of evidence suggest that predation dynamics in prehistoric ecosystems differed substantially from extant ones. Communities of Quaternary mammals were represented by species with no extant analogues, such as predatory saber-toothed cats, giant hyenas, or large megaherbivores such as the woolly mammoth. Possible specialization on juvenile megaherbivores by large predators (e.g., saber-toothed cats) has been proposed (Turner and Antón, 1997; Arribas and Palmqvist, 1998; Palmqvist et al., 1996, 2003, 2008) even if analyses of functional morphology challenge this conclusion (cf., McHenry et al., 2007; Andersson et al., 2011). Regardless of whether this phenomenon was likely to occur, there is no support to suggest that large predators controlled megaherbivore populations in Quaternary ecosystems.

Herein, we attempt to quantify biomass fluxes in Quaternary ecosystems on the Italian peninsula. Studies based on extant ecosystems suggest that the biomass of large mammalian herbivores is generally controlled by rainfall and vegetation productivity (Coe et al., 1976; East, 1984; Sinclair, 2003; Owen-Smith and Mills, 2006; Pettorelli et al., 2009). In turn, biomass of predators is regulated by the biomass of their favorite prey (East, 1984; Carbone and Gittleman, 2002; Woodroffe and Ginsberg, 2005; Hayward et al., 2007; Owen-Smith and Mills, 2008a, 2008b; Carbone et al., 2011).

Population density data in recent ecosystems allow accurate estimates of mammal biomass from different extant ecosystems to be made. However, similar quantification is problematic for fossil ecosystems where population density can only be inferred (Damuth, 1982). Barnosky (2008) recently explored biomass fluctuations in Plio-Pleistocene ecosystems worldwide. Based on estimated population density of fossil species, he demonstrated that biomass relationships have changed since the arrival of early humans so that the megafauna (defined as mammals bigger than 44 kg) biomass decreased as the human population increased. This approach provides the incentive to explore biomass fluctuations in fossil mammal communities in more detail.

The goals of this manuscript are to: (1) quantify the biomass of large mammals in the Plio-Pleistocene of Italy; and (2) identify biomass flux from prey to predators in terms of the relationship of their respective biomasses.

The Italian fossil record is ideal for these purposes because it has been intensively investigated, and both species taxonomy and occurrences are well established (Raia et al., 2005, 2006a, 2006b; Meloro et al., 2007, 2008). Raia et al. (2007) and Meloro et al. (2007) have already explored predator-prey dynamics in Italian Plio-Pleistocene fossil assemblages, demonstrating that communities between 3.2 and 1.0 Ma were predation controlled because of the high number of large carnivore species relative to ungulate species. Later communities (1.0 – 0.3 Ma) were more resource controlled because the number of species of megaherbivores increased relative to the other herbivore taxa. However, Meloro et al. (2008) cautioned against the interpretation of

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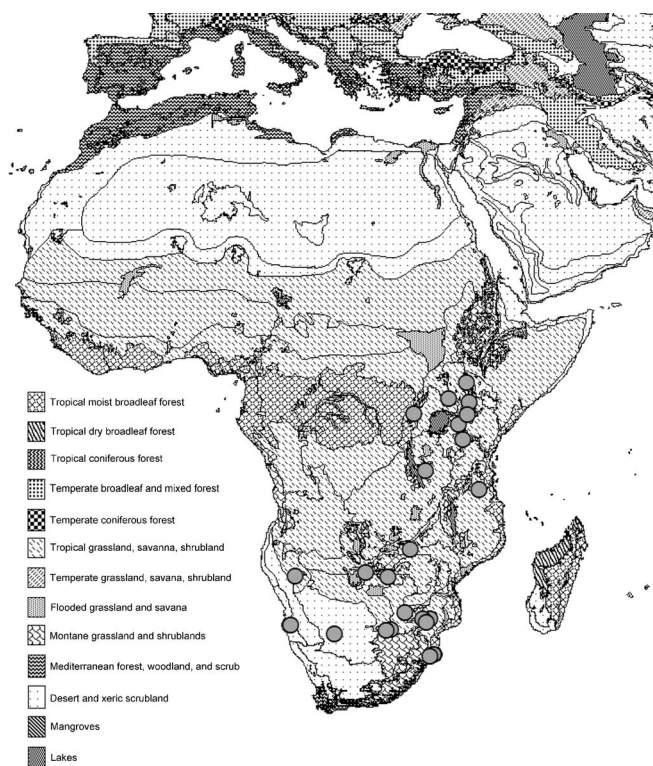


FIGURE 1—Geographic distribution of extant African ecosystems (gray circles), based on appendix data from Hayward et al. (2007). Biome distribution is also displayed; the majority of sampled ecosystems belong to tropical grassland, savanna, scrubland.

Plio-Pleistocene large mammal diversity because it is taphonomically biased at all trophic levels. Indeed, carnivore, as well as herbivore, diversity remained constant and only turnover rates effectively changed through time, likely as a function of climatic changes. In the present study, rather than using species diversity, we quantify the fossil predator-prey biomass to promote an alternative way to interpret ecosystem dynamics from the fossil record.

Studies based on extant ecosystems suggest that a strong relationship should occur between the biomass of prey (defined as ungulate species smaller than 450 kg, cf., Estes, 1984) and predators. Here, we test this hypothesis using the Italian fossil record, considering for the first time different definitions of prey. Indeed, large herbivore prey could be split into species <450 kg or species <1000 kg (according to the megaherbivore definition, Owen-Smith, 1988). If predator biomass is solely influenced by prey biomass we should find no differences when comparing data from extant populations with relationships estimated for Plio-Pleistocene ecosystems.

MATERIALS AND METHODS

Datasets

Data, as presented in Hayward et al. (2007), are used to quantify and compare predator-prey biomass values of 33 extant African localities (Fig. 1) with nine Italian Plio-Pleistocene large mammal communities (Figs. 2, 3). The Hayward et al. (2007) record was preferred to others (e.g., Schaller, 1972; or Estes, 1984) because it presents population density data (=number of individuals per km²) for all herbivores (belonging to Artiodactyla, Perissodactyla, and Proboscidea) within the communities. In this way, it is possible to explore the effect of different prey definitions by including or excluding specific taxa from the analyses. Additionally, the Hayward et al. (2007) dataset is one of the most updated records for the African national parks, with several



FIGURE 2—Geographic distribution of Italian local fossil assemblages grouped into three major temporal divisions: Villafranchian (black circles) including PCOMs Triversa, Montopoli, Up Valdarno, Val di Chiana, and Pirro; Galerian (white triangles) inclusive of PCOMs Galerian 1, 2, and 3; and Aurelian (gray circles). The sea locality (gray dot close to the south Tyrrhenian coastline) is the small island of Capri, where the Quisisana large mammal fauna came from.

temporal series for the same localities (e.g., Serengeti census data are available for 1966–1967 and the 1990s). Within this record, predator density data exist only for carnivores bigger than 21 kg (Carbone et al., 1999). This includes lion *Panthera leo*, leopard *P. pardus*, cheetah *Acinonyx jubatus*, spotted hyena *Crocuta crocuta*, and African wild dog *Lycaon pictus*.

Raia et al. (2005, 2006a) subdivided Italian Plio-Pleistocene mammal communities (from 3.2 until 0.3 Ma) into 9 distinct paleocommunities (PCOMs), each including a different number of Local Assemblages (LAs): Triversa (2 LAs, 3.2 Ma), Montopoli (5 LAs, 2.6 Ma), Upper Valdarno (14 LAs, 1.9 Ma), Val di Chiana (5 LAs, 1.5 Ma), Pirro (5 LAs, 1.1 Ma), Galerian 1 (6 LAs, 0.8 Ma), Galerian 2 (5 LAs, 0.6 Ma), Galerian 3 (8 LAs, 0.45 Ma), and Aurelian (22 LAs, 0.3 Ma) (Figs. 2, 3). These biochronological units resemble extant ecosystems with respect to distribution of species abundance (Raia et al., 2006b) and they facilitate the identification of communities of interacting species (Meloro et al., 2007, 2008).

Meloro et al. (2007) estimated body mass (based on craniodental measurements) and theoretical population density data in large fossil mammals (>7 kg) of each PCOM (based on equations in Silva and Downing, 1995: for herbivores, $\log y = -0.44 \log x + 1.01$; for carnivores, $\log y = -1.31 \log x + 1.22$; x is equal to body mass in kilogram). We are using that record (Appendix in Meloro et al., 2007) to compute biomass values for both predator and prey communities. Conservatively, all omnivorous bears (*Ursus* spp.) were excluded from the predatory guild according to a recent palaeoecological interpretation based on ecomorphology (Meloro, 2011a, 2011b), and only carnivores whose estimated body mass was bigger than 21 kg were considered.

Statistical Analyses

Biomass values are computed for different categories (predators or prey) of large mammals in both extant and fossil ecosystems. Species body mass (in kg) is multiplied by the number of individuals per km² (as

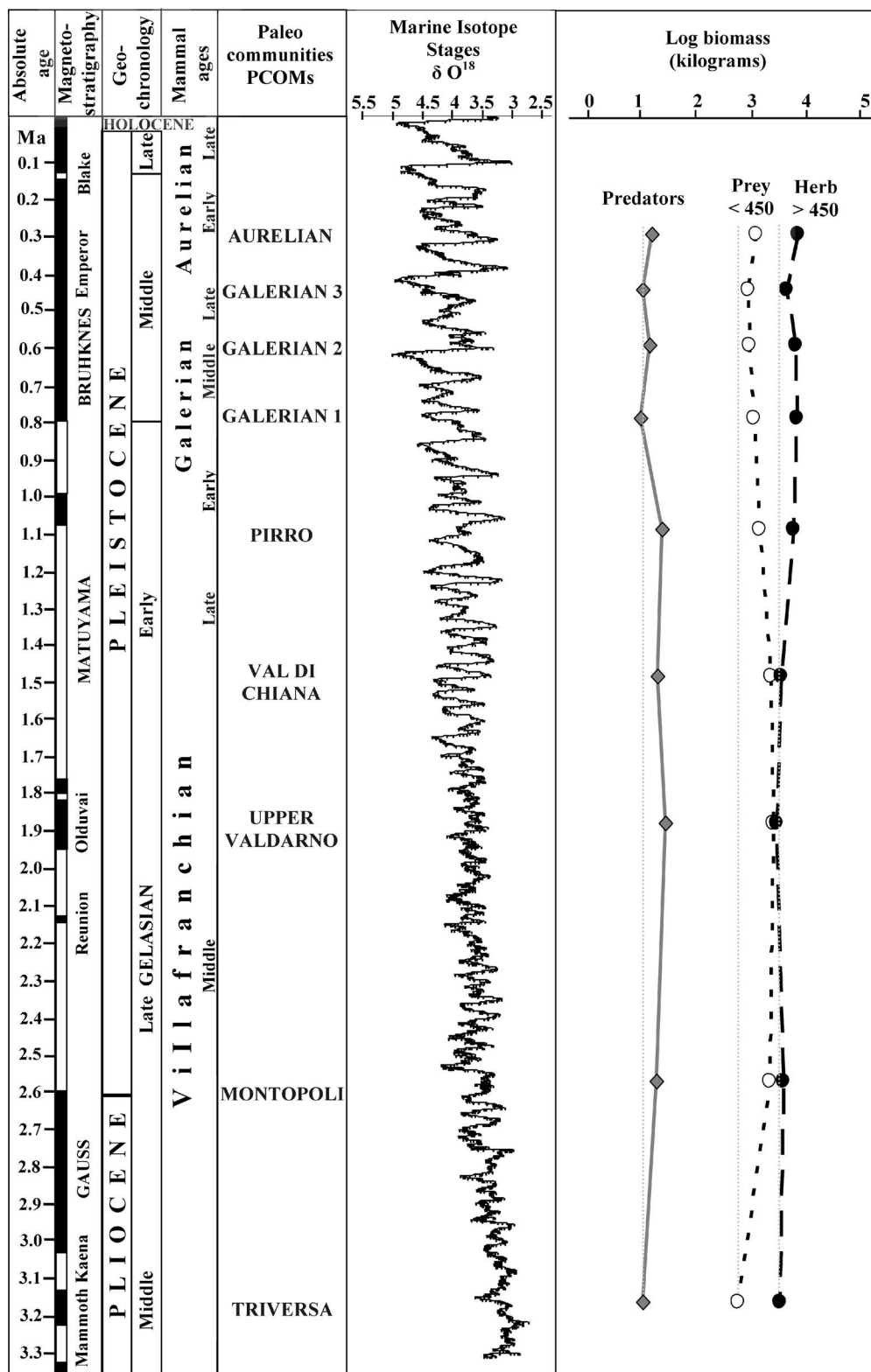


FIGURE 3—Biochronological framework of Italian paleocommunities (PCOMs). Trends of temporal changes in log transformed biomass values (in kilograms) are shown for predators, prey <450 kg, and herbivores >450 kg. Thin gray lines are for reference.

given for extant ecosystems, or as estimated using the body mass–population density equations) and then summed to match the category of interest. To explore the hypothesis of different prey definitions we quantified herbivore biomass for species with a body mass smaller than 450 kg as well as species with a body mass below 1000 kg (Estes, 1984; Owen-Smith, 1988).

The biomass data, reported in kg, were log transformed and relationships between prey biomass (independent variable) and predator biomass (dependent variable) were tested via Ordinary Least Square (OLS). Extant ecosystems were considered separately from fossil ones and tests for differences in slope are employed to identify similarity or dissimilarities in predator-prey dynamics.

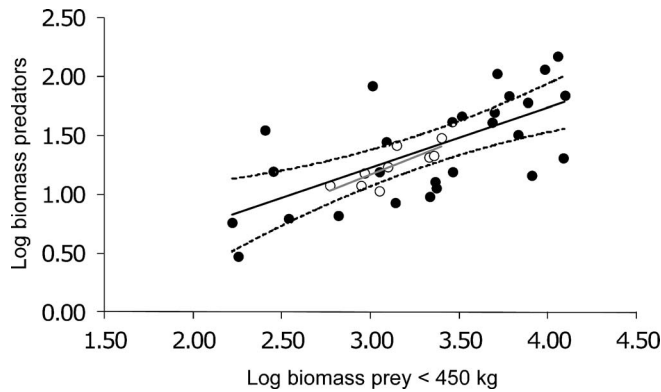


FIGURE 4—Scatter plot of log transformed biomass prey (<450 kg) versus biomass of predators. Black circles represent extant African ecosystem, and white circles are Plio-Pleistocene community from Italian peninsula. Regression trendline for extant ecosystems (solid black line) with mean confidence intervals (dashed line), and regression trendline for Plio-Pleistocene communities (solid gray line). The equation for extant communities is $y = 0.512x - 0.312$, $R^2 = 0.439$; the equation for Plio-Pleistocene communities is $y = 0.610x - 0.664$, $R^2 = 0.650$.

We identified five outliers in extant ecosystems due to their unusually small values in predator biomass and analyses were repeated, both with, and without including them. No differences occur in the general results, and we here present available data without outliers ($N = 28$ reduced from the original record of 33).

RESULTS

Biomass in the Plio-Pleistocene

Biomass estimates of different trophic levels are not correlated to number of local assemblages within each PCOM (non-parametric correlation $P > 0.10$). This ensures that biomass values are unaffected by the sample size of fossil localities. Total mammal biomass is relatively stable throughout the Plio-Pleistocene (Fig. 3). When considering different trophic levels, a sharp decline occurs during Galerian 2 for medium-sized ungulates <450 kg. Also predator biomass shows two declining phases at Galerian 1 and 3. On the other hand, the biomass of herbivores >450 kg increased from Pirro until Aurelian. The same trend on temporal scale occurs when herbivores are split into < or >1000 kg.

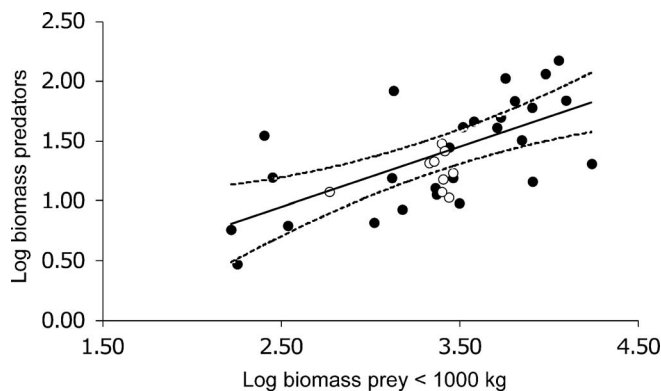


FIGURE 5—Scatter plot of log transformed biomass prey (<1000 kg) vs biomass of predators. Black circles represent extant African ecosystem while white circles are Plio-Pleistocene community from Italian peninsula. Regression trendline with mean confidence intervals (in dash) is displayed for extant ecosystem only. The equation for extant communities is $y = 0.503x - 0.307$, $R^2 = 0.425$.

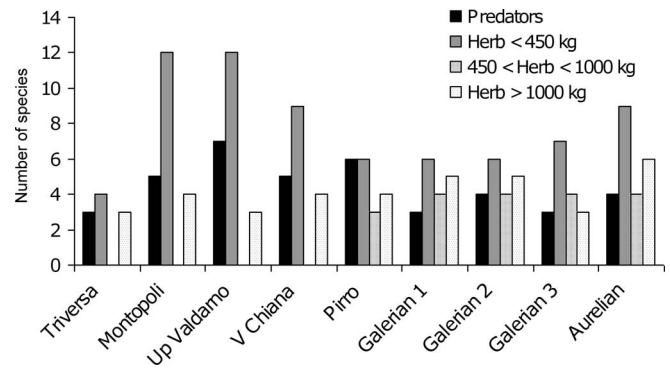


FIGURE 6—Number of predators and of different class sizes of large herbivore species through paleocommunities in Italy from the oldest (Triversa, 3.2 Ma) to the youngest (Aurelian, 0.3 Ma).

Predator-Prey Biomass

There is a positive association between prey (<450 kg) and predator biomass in extant as well as fossil ecosystems (Fig. 4). The association in the extant species dataset is not isometric and suggests a lower increase in predator biomass relative to prey biomass ($b = 0.512$, CI 95% = 0.273 – 0.750, $p < 0.0001$). OLS records a significant positive slope also for the Plio-Pleistocene record ($b = 0.610$; CI 95% = 0.210 – 1.01, $p = 0.009$) that is not statistically different from that of extant ecosystems ($F = 0.035$, $p = 0.853$).

A positive relationship occurs also when prey are classified as species <1000 kg in extant ecosystems (Fig. 5). The slope is again not isometric ($b = 0.503$, CI = 0.262 – 0.743, $p < 0.0001$) and is very similar to that observed when prey are considered as only ungulates <450 kg. However, no association occurs when this prey category is applied to Plio-Pleistocene communities (Fig. 5). The slope is not significantly different from zero with ($b = 0.260$, CI = -0.373 – 0.892, $p = 0.364$) or without ($b = -0.165$, CI = -2.608 – 2.278, $p = 0.874$) the inclusion of one outlier (PCOM Triversa).

The Role of Larger Herbivores

In extant ecosystems, the biomass of large herbivores (>450 kg or >1000 kg) is not always associated to the biomass of smaller herbivores or predators (non-parametric correlation, $P > 0.10$). The same applies for fossil ecosystems. However, large ungulates whose body mass ranged between 450 and 1000 kg appear only after the PCOM Val di Chiana (1.5 Ma) (Fig. 6). The number of herbivores bigger than 450 kg increased between Villafranchian (mean 4.2) and Galerian-Aurelian (mean 8.5) PCOMs (Mann-Whitney $Z = -2.233$, $p = 0.024$). The same is not valid for herbivores >1000 kg only ($p = 0.20$).

The relative biomass of large herbivores (between 450 and 1000 kg) constitutes a similar proportion in both prehistoric and extant ecosystems ($N = 9$, mean prehistoric = 11.3% [0%–32%]; $N = 28$, mean extant = 8.3% [0%–55%]; Mann Whitney $U = 104.0$, $Z = -0.670$, $p = 0.541$). The same applies when ecosystems with no large herbivores are excluded ($N = 5$, mean prehistoric = 20.4% [17%–32%]; $N = 15$, mean extant = 14.9% [4%–55%]; Mann Whitney $U = 20.0$, $Z = -1.53$, $p = 0.142$).

DISCUSSION

Biomass in Extant Ecosystems

Most of the ecological research has focused on the relationship between the biomass of prey and that of specific predators (Schaller, 1972; Kruuk, 1972; Estes, 1984; Carbone and Gittleman, 2002; Fuller et al., 2003; Hayward et al., 2007; Wegge et al., 2009; Carbone et al.,

2011). Only Estes (1984) and Skogland (1991) attempted to explore the biomass of the entire predatory guild in relation to their prey. The slope we find using the Hayward et al. (2007) dataset is in agreement with that presented in these previous studies. Indeed, Estes (1984) data show, on a log scale, a slope of 0.66, while Skogland (1991) presented a slope of 0.56 when including a variety of ecosystems from the arctic to equatorial latitudes. Both values are similar to the 0.512 slope presented in our study.

Interestingly, the presented predator-prey biomass slope did not change significantly when using a different definition of prey (<450 kg, or <1000 kg) in extant African ecosystems. This effect is determined by the strong predominance, in biomass proportion, of medium-sized ungulates (<450 kg) that constitute, on average, 83% of the overall large mammal biomass. Large herbivores between 450 and 1000 kg are represented by a poor diversity of taxa (only the giraffe and the hippopotamus in the sample of extant ecosystems) whose proportional biomass tends to be less than 10%. Large carnivores rarely prey upon these taxa, although Owen-Smith and Mills (2008a) reported giraffe as potentially limited by lion predation in some South African ecosystems. Lions, as the largest predator of the African savannah, also regulate the entire biomass flux in several ecosystems because their flexible dietary preference impacts the prey populations as a whole (Owen-Smith and Mills, 2008a, 2008b). However, this impact changes significantly with rainfall conditions. When the population of the lions' favorite prey are less susceptible to being killed (e.g., wildebeest and zebras under conditions of low rainfall), alternative prey are selected and their populations limited.

This pattern suggests that a complex interplay occurs between primary resources, herbivorous prey and carnivorous consumer, so that ecosystems may clearly switch from one state to another. Recently, Fritz et al. (2011) presented a more sophisticated mammal food web for African savannas suggesting an even more limited category of prey classes as identified by species smaller than 150 kg. These species are supposed to be more responsive to predator control and seem to be less food limited. However, this model is inapplicable when comparing extant with fossil ecosystems in the study area. Indeed, during the Italian Quaternary several herbivore communities were broadly dominated by species bigger than 150 kg so that smaller ungulates represented less than 10% of prey diversity in some assemblages (Raia et al., 2007; Meloro et al., 2007).

Biomass in Quaternary Communities

Even though our population density data are only theoretical estimates, they suggest that a genuine association between prey (<450 kg) and predator biomass applies to Quaternary fossil communities from the Italian peninsula. Additionally, no difference in slope occurs between the Plio-Pleistocene fauna and extant ecosystems. This similarity is even more striking if we consider that the slope obtained for the Quaternary dataset (0.61) is very similar to those presented by Estes (1984) and Skogland (1991). This result gives us confidence that predator-prey dynamics between extant and fossil communities are comparable within the range of medium-sized ungulates. There is strong taphonomic and theoretical evidence that this category of ungulate was more likely to be affected by predation during the Quaternary on the Italian peninsula (Mazza et al., 2004; Mazza, 2006; Meloro et al., 2007; Raia et al., 2007). On the other hand, no association occurred in the fossil record when prey are defined as all species <1000 kg. Such dissimilarity suggests that ungulate communities within the range of 450–1000 kg may have differed from those in extant ecosystems, particularly in terms of susceptibility to predation.

The peculiar status of ungulate species weighing between 450 and 1000 kg is also emphasized by the fact that they appear only after the Val di Chiana, a community that occurred at 1.5 Ma and thus precedes the strong climatic oscillation that occurred during the middle to Late

Pleistocene (Meloro et al., 2008). This category almost exclusively includes grazers belonging to the genera *Equus*, *Bison*, and *Bos*, and their role as key prey is debatable (cf., Meloro et al., 2007). Diedrich (2010, 2011) suggests that Pleistocene hyenas, and possibly lions, specialized on horse hunting in Germany. However, Bocherens et al. (2011) provided evidence for a strong specialization on reindeer by Pleistocene lions in several European fossil localities before their extinction (around 25,000 bp), while communities of wolves and hyenas from Mediterranean localities tended to be generalist predators (hunting the more abundant taxa like red deer), even if this implies trophic overlap (Stiner, 1992; Feranec et al., 2010). These findings are compatible with the concept that herbivores between 450 and 1000 kg were not the main prey items for large carnivores. Thus, the alternative explanation, that carnivore density rather than carnivore diversity increased as a reaction to the increasing biomass of large herbivores, is rendered less likely.

The diversity of this herbivore size class during the coldest phase of the Quaternary is symptomatic of important structural changes to the ecosystems through time. Indeed, their increase in species number was directly related to changes in climatic conditions in Italy (Raia et al., 2007). The unusual proportion of herbivore biomass relative to predators suggests also that important changes occurred in the latter guild. Changes in guild structure of Italian predators during the middle Pleistocene have been widely recognized (Palombo and Mussi, 2006; Meloro et al., 2007; Palombo, 2010; Meloro, 2011b, 2011c), and they provide a link to understanding the invasion by early humans. Large predators that dominated the late Pliocene-early Pleistocene (long-canine cats, giant hyenas) were replaced by a lower number of predators (including pantherine cats, the spotted hyena, and the gray wolf) that were more adapted to colder climatic conditions and to the expansion of boreal-temperate forests (Raia, 2010; Meloro, 2011a, 2011b). Human occupation became increasingly important during the middle Pleistocene. Human impact on populations of large herbivores was likely significant. Multiple lines of evidence from the Italian and French fossil records support predation by humans on juvenile bison and auroch (*Bos primigenius*) and possibly also large proboscideans (Mussi and Villa, 2008; Hohenstein et al., 2009; Boschian and Saccà, 2010; Rendu, 2010). Thus, our theoretical biomass estimates suggest that significant changes occurred in predatory guild structure by the end of the early Pleistocene to justify the arrival and expansion of the human predatory niche. However, this does not necessarily imply that humans caused a decrease in large ungulate diversity and density. Indeed, based on the Italian fossil record, Meloro et al. (2007) reported a high abundance of Pleistocene bison and horses after controlling for the theoretical predation pressure. This provides further support for the lack of association between predator and prey, as defined as species <1000 kg, due to structural changes of the whole large mammal community. This in turn implies a possible switch in the way ecosystems functioned, from top-down to bottom-up controlled (cf., Meloro et al., 2007, 2008; Raia et al., 2007; Raia, 2010).

CONCLUSIONS

The analysis of theoretical biomass provides an excellent tool for investigating the structure of mammalian communities in ancient ecosystems. These analyses represent important baselines to which fossil-based abundance estimates can be compared, and provide evidence for similarities in biomass flux at certain trophic levels.

We demonstrate that recent mammal communities and Italian Plio-Pleistocene fossil communities are similar in predator-prey biomass fluctuations, when prey are defined as herbivores smaller than 450 kg. However, differences emerge when prey species smaller than 1000 kg are considered. Plio-Pleistocene herbivores weighing between 450 and 1000 kg increase in number after the middle Pleistocene as a response to climatic changes, and they generate an imbalance in predator-prey biomasses that is not detected in recent ecosystems.

We emphasize the necessity of providing a robust definition when identifying predators and prey in both extant and fossil mammalian communities, because prey categories, such as those based on body mass estimates in this study, may differ between extant and fossil ecosystems. By identifying these differences, the fossil record provides insight into the evolution of predator-prey interactions in present-day communities.

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